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A MULTIVARIATE MORPHOMETRIC STUDY OF THE *SOLIDAGO CANADENSIS* / *S. LEPIDA* COMPLEX OF *SOLIDAGO* SUBSECT. *TRIPLINERVIAE*. I. NORTHEASTERN TAXA (ASTERACEAE: ASTEREAE)

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ABSTRACT

The *Solidago canadensis*/*S. lepida* complex stretches across much of North America. A multivariate morphometric analysis including 28 vegetative and floral traits scored on 162 specimens was performed to assess the classification of the complex in eastern North America proposed by Semple (2013). Discriminant analysis indicates support for recognizing the following taxa: *Solidago elongata* and *S. lepida* in western North America and *S. brendiae, S. canadensis* (var. *canadensis* and var. *hargeri)*, and *S. fallax* (var. *fallax* and var. *molina*) in eastern North America.

KEY WORDS: *Solidago canadensis, Solidago lepida, Solidago brendiae, Solidago elongata, Solidago fallax, Solidago* subsect. *Triplinerviae*

The *Solidago canadensis* L./ *S. lepida* DC. complex occurs across much of North America (Semple & Cook 2006). Taxonomic treatments of the complex have differed greatly in how many taxa are to be recognized and at what taxonomic rank. Fernald (1915) described two varieties as *S. lepida* var. *fallax* Fern. and *S. lepida* var. *molina* Fern., and he treated *S. elongata* Nutt. as *S. lepida* var. *elongata* (Nutt.) Fern. In the same paper, Fernald also described a hairy-stemmed, more southern race as *S. canadensis* var. *hargeri* Fern. The complex also includes *S. gigantea* Ait. Melville and Morton (1982) presented a multivariate study of the eastern taxa of the complex focusing only on those occurring in Ontario. They found support for recognizing the two varieties of *S. canadensis*: *S. lepida* at specific rank, and *S. gigantea*. Cronquist (1994) treated *S. lepida* as *S. canadenis* var. *lepida* (DC.) Cronq., and he noted that *S. gigantea* was an easily recognized species separate from the *S. canadensis* complex.

In the Flora of North America, Semple and Cook (2006) followed Melville and Morton on *Solidago canadensis*, recognized *S. lepida* subsp. *fallax* (Fern.) Semple with Fernald's two varieties in synonymy, restricted *S. elongata* to the Pacific Coast states from Washington to California, and treated *S. gigantea* as a separate species. Semple (2013) treated Fernald's eastern varieties of *S. lepida* as *S. fallax* var. *fallax* and *S. fallax* var. *molina* (Fern.) Semple and Fernald's "*elongata*" as a new species *S. brendiae* Semple.

Also included in the *Solidago canadensis/lepida* complex are the western *S. lepida* var. *salebrosa* (Piper) Semple and *Solidago rupestris* Raf., which along with *S. gigantea* are not covered in the multivariate analysis presented below. Other species of *Solidago* subsect. *Triplinerivae* (Torr. & A. Gray) Nesom are included in the informal *Tortifolia* Group (Semple, Astereae Lab web site, continuously updated) and are not included in the multivariate analysis presented below. Additional multivariate morphometric studies in preparation by the Astereae Lab will cover taxa not included below.

MATERIALS AND METHODS

In total, 162 specimens from BOON, MIN, JKM in ROM, and WAT in MT (Thiers, continuously updated) were selected for inclusion in the analysis of northeastern North American taxa from a matrix of 280 plants covering the entire transcontinental *Solidago canadensis/lepida* complex. Thirteen vegetative and 15 floral traits were scored for each specimen: 1–5 replicates per character depending upon availability of material and whether or not the trait was meristic (Table 1). Mean values were used in the analyses, while raw values were used to generate ranges of variation for each trait. Sample sizes varied among taxa based on the size of the range of distribution and availability of specimens: 27 *S. brendiae,* 30 *S. canadensis var. canadensis,* 12 *S. canadensis var. hargeri,* 26 S. *elongata,* 12 S. *fallax* var. *fallax,* 11 S. *fallax* var. *molina,* and 27 *S. lepida var. lepida*; one additional specimen was included by not assigned to an a priori group.

Table 1. All characters scored on specimens included in the study *S. canadensis/S. lepida* complex; traits scored in replicates of five when material available; 1 value for meristic traits.

STMHT	Height of the stem from base to the top of the inflorescence (cm)
LLFN	Lower stem leaf length (mm)
LLFW	Lower stem leaf length (mm)
LLFWTOE	Length of lower stem leaf from widest point to tip (mm)
LLFSERNUM	Number of serrations on one side of a lower stem leaf (side with the most)
MLFLN	Mid stem leaf length (mm)
MLFW	Mid stem leaf width (mm)
MLFWTOE	Length of mid stem leaf from widest point to tip (mm)
MLFSERNUM	Number of serrations on one side of a mid stem leaf (side with the most)
ULFLN	Upper stem leaf length (mm)
ULFW	Upper stem leaf width (mm)
ULFWTOE	Length of upper stem leaf from widest point to tip (mm)
ULFSERNUM	Number of serrations on one side of a upper stem leaf (side with the most)
CAPL	Length of inflorescence from tip to base of lowest branch (cm)
CAPW	Width of pressed and dried inflorescence at widest point (cm
INVOLHT	Height of involucre from base to tip of longest phyllary (mm)
OPHYLL	Length of outer phyllary (mm)
IPHYLL	Length of inner phyllary (mm)
RAYNUM	Number of ray florets
RSTRAPL	Length of the ray strap (lamina; mm)
RSTRAPWD	Width of the ray strap (lamina; mm)
RACHBL	Length of the ray floret ovary at anthesis (mm)
RPAPL	Length of the ray floret pappus at anthesis (mm)
DISCNUM	Number of disc florets
DCORL	Length of the disc floret corolla in total (mm)
DLOBL	Length of the disc floret lobes (mm)
DACHBL	Length of the ray floret ovary at anthesis (mm)
DPAPL	Length of the ray floret pappus at anthesis (mm)

Traits used to define a priori groups were not included in the analyses to avoid circular logic. Differences in general inflorescence shape and branching characteristics, lower stem pubescence density, and leaf pubescence density were used to define a priori groups along with geographic location.

All analyses were performed using SYSTAT v.10 (SPSS 2000). A pair-wise Pearson correlation matrix was created to determine which characters were highly correlated. One trait of each pair that had a $> |0.7|$ correlation value was excluded from the analysis to avoid possible

pleiotropic effects of a single gene and to make the tests of null hypothesis more stringent. Stepwise discriminant analysis (STEPDISC) was used to select traits that best separated groups based on the Mahalanobis distances between a priori group centroids.

Classificatory Discriminant Analysis was run on N-1 traits selected by the STEPDISC analysis, if more than N-1 traits were selected, where N = lowest sample size of the a priori groups; in this study N = 11. Geisser probabilities of assignment to each a priori group were generated for each specimen a posteriori based on the Mahalanobis distances from the specimen location plotted in N-dimensional hyperspace to each a priori group centroid. Linear and Jackknifed analyses were run in each classificatory analysis to test the strength of group separation in terms of the numbers of discriminating traits. Results are presented in the form of 1) F-value matrices based on Mahalanobis distances between group centroids and 2) tables summarizing the results of the two methods of doing the classificatory discriminant analyses. Conclusions were reached based on the percent of correct placements of specimens and the probabilities of the placements being correct and visual re-examination of each specimen initially and latter higher resolution digital images of the specimens. Lastly, a canonical analysis was performed as a dimension reduction technique to allow visualization of results in 1 to 3 dimensions with the number of dimensions being N-1, where in this case N equals the number of a priori groups in an analysis.

Six separate discriminant analyses were performed. The first was performed on seven a priori groups and included 162 specimens assigned to one of the a priori groups; one additional specimen was included but not assigned to an a priori group. A second analysis was performed on two a priori groups of just specimens of *Solidago brendiae* and *S. canadensis*. A third analysis was performed on three a priori groups of just specimens of *S. brendiae*, *S. canadensis* var. *canadensis*, and *S. canadensis* var. *hargeri*. A fourth analysis was performed on two a priori groups of just specimens of *S. brendiae* and *S. fallax*. A fifth analysis was performed on three a priori groups of just specimens of *S. brendiae*, *S. fallax* var. *fallax*, and *S. fallax* var. *molina*. A sixth analysis was performed on two a priori groups of just specimens of *S. canadensis* var. *canadensis* and *S. canadensis* var. *hargeri*.

RESULTS

Seven taxa analysis

Data on all specimens were used to generate a Pearson Correlation Matrix. The following pairs of traits had correlations greater than |0.7|: MLFLN–ULFLN, MLFW–UPLWF, CAPL–CAPW, INVOLHT–DCORL, IPHYLL–RPAPL, IPHYLL–DCORL, RPAPL–DCORL, RPAPL–DPAPL, and DCORL–DPAPL. MLFL, UPLW, IPHYLL, DCORL and DPAPL were excluded in the discriminant analyses. CAPL and CAPW were also excluded as these were used to partially define a priori groups. Stepwise discriminant analysis selected the following seven traits as useful in separating the a priori groups in the analysis including all taxa: RPAPL (17.01), RAYNUM (12.35), ULFLN (10.83), MLFW (7.19), INVOLHT (7.04), DISCNUM (5.60), and DLOBL (5.39) in decreasing order of F-to-remove value. Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2.

In the Classificatory Discriminant Analysis, correct assignments of specimens for taxa ranged from 63% to 96%. The Classification matrix and Jackknife classification matrix are presented in Table 3 and the Geisser assignment probabilities by taxon to a posteriori taxa are summarized in Table 4. Individual a priori taxa are presented below in decreasing order of percent correct placement.

* Twenty-five of the 26 specimens (96%) assigned a priori to the western *Solidago elongata* were placed a posteriori into *S. elongata* with 15 specimens placed with 90-100% probability; the mean assignment

probability was 84%. Two of collections assigned a posteriori to *S. elongata* were from southwestern British Columbia: Murrin Prov. Pk., *Lomer 6361* (UBC); Surrey, *Lomer 6467* (UBC).

* Twenty-three of the 27 specimens (89%) assigned a priori to *Solidago brendiae* were placed a posteriori in *S. brendiae* with 11 specimens placed with 90-100% probability; the mean assignment probability was 70%. Of the three specimens not assigned a posterieri to *S. brendiae*, one was assigned to *S. canadensis* var. *canadensis* with 33% probability, one was assigned to *S. canadensis* var. *hargeri* with 49% probability, and one was assigned to *S. fallax* var. *fallax* with 62% probability.

* Twenty-six of the 30 specimens (87%) assigned a priori to *Solidago canadensis* var. *canadensis* were placed a posteriori in var. *canadensis*; six specimens with 87-100% probability, 15 specimens with 60-79% probability; and five with 50-59% probability; the mean assignment probability was 65%. Of the four specimens not placed in var. *canadensis*, one was placed in var. *hargeri* with 66% probability, two were placed in *S. brendiae* with 49% and 81% probability, and one was placed in *S. elongata* with 68% probability.

* Sixteen of the 21 specimens (76%) assigned a priori to *Solidago canadensis* var. *hargeri* were placed a posteriori in var. *hargeri*; four specimens with 90-100% probability, four specimens with 80-89% probability, five specimens with 69-79% probability, and three specimens with 41-49% probability; the mean assignment probability was 65%. Of the five specimens not placed in var. *hargeri*, four were placed in var. *canadensis* with 44-73% probability and one was placed in *S. brendiae* with 97% probability. One of the two field collected specimens of *S. canadensis* var. *hargeri* from Europe was assigned a posteriori to var. *hargeri* with 41% probability; the other was assigned a posteriori to var. *canadensis* with 58% probability.

* Eight of the 12 specimens (67%) assigned a priori to the *Solidago fallax* var. *fallax* were placed a posteriori into var. *fallax*; 4 specimens with 81-95% probability, three with 75-77% probability and two with 52-53% probability; the mean assignment probability was 63%. Of the four specimens not placed in var. *fallax*, one was placed in var. *molina* with 60% probability, one was placed in *S. brendiae* with 49% probability, and one was placed in *S. lepida* with 36% probability (32% in var. *fallax* and 31% in var. *molina*), and one in *S. canadensis* var. *hargeri* with 38% probability (27% t0 var. molina and 22% to var. *fallax*).

* Twelve of the 19 specimens (63%) assigned a priori to the *Solidago fallax* var. *molina* were placed a posteriori into var. *molina*; 1 specimen with 97% probability, four with 74-88% probability, four with 57-64% probability, and one with 40% probability; the mean assignment probability was 50%. Of the seven specimens were not placed in var. *molina* a posteriori, three were placed in var. *fallax* with 85%, 53% and 42% probability, two were placed in *S. brendiae* with 62% and 46% probability, and two were placed in *S. elongata* with 50% and 41% probability.

* Seventeen of the 27 specimens (63%) assigned a priori to the *Solidago lepida* var. *lepida* were placed a posteriori into var. *lepida*; 14 specimens with 90-100% probability, two with 72-81% probability, and one with 53% probability; the mean assignment probability was 60%. Of the 10 specimens not placed in *S. lepida* var. *lepida*, one specimen from northern Ontario was placed in *S. elongata* with 98% probability, four specimens were placed in *S. elongata* with 47-69% probability, one diploid specimen from the Northwest Territories in western Canada was placed in *S. brendiae* with 46% probability, one specimen was placed in *S. fallax* var. *molina* with 46% probability (45% to S. lepida), and three specimens were placed in *S. fallax* var. *fallax* with 73%, 64% and 39% probabilities, respectively with the first two of these being hexaploids from British Columbia.

Table. 2. Between Group F-matrix for the seven taxa analysis; df = 7, 145

	brendiae	*canadensis*	*elongata*	*fallax*	*hargeri*	*lepida*
canadensis	15.713	0.000				
elongata	21.500	24.660	0.000			
fallax	6.286	15.238	15.284	0.000		
hargeri	17.938	5.450	27.342	11.914	0.000	
lepida	30.280	50.234	17.410	11.119	36.769	0.000
molina	11.686	13.959	11.274	3.212	12.446	10.261

Wilks' lambda = 0.0481, df = 7, 6, 155; approx. F= 15.1988, df = 42, 702; prob = 0.0000

Table 3. Results of the Classificatory Discriminant Analysis of the *S. canadensis/S. lepida* complex.

Classification matrix (a priori assignments in rows, a posteriori assignments in columns)

	brendiae	*canadensis*	*elongata*	*fallax*	*hargeri*	*lepida*	*molina*	% correct
brendiae	24	1	0	1	1	0	0	89
canadensis	2	26	0	0	1	0	0	87
elongata	0	1	25	0	0	0	0	96
fallax	1	0	0	8	1	1	1	67
hargeri	1	4	0	0	16	0	0	76
lepida	1	0	5	3	0	17	1	63
molina	1	0	2	3	0	1	12	63
Totals	30	32	33	15	19	19	14	79

Jackknifed classification matrix

	brendiae	*canadensis*	*elongata*	*fallax*	*hargeri*	*lepida*	*molina*	% correct
brendiae	23	1	0	1	2	0	1	85
canadensis	2	25	1	0	2	0	0	83
elongata	0	2	24	0	0	0	1	92
fallax	2	0	0	8	2	1	1	67
hargeri	2	4	0	0	14	0	2	67
lepida	2	0	6	3	0	16	1	59
molina	2	0	3	3	0	1	11	58
Total	29	31	34	15	16	18	17	75

Table 4. Summary of mean values of Geisser assignment probabilities for each taxon to taxon:

	brendiae	*canadensis*	*hargeri*	*elongata*	*fallax*	*molina*	*lepida*
S. brendiae	**70%**	6%	5%	3%	9%	7%	1%
S. canadensis							
var. *canadensis*	8%	**65%**	19%	3%	0%	4%	0%
var. *hargeri*	6%	23%	**65%**	1%	1%	5%	0%
S. elongata	2%	3%	2%	**84%**	0%	6%	3%
S. fallax							
var. *fallax*	11%	1%	4%	0%	**63%**	18%	4%
var. *molina*	5%	4%	4%	10%	19%	**50%**	8%
S. lepida	2%	0%	0%	15%	8%	9%	**66%**

In the Jackknifed Classificatory Discriminant Analysis, correct assignments did not change or changed little from the linear Classificatory Discriminant Analysis. On average the decrease was 4%, with no change *Solidago fallax* var. *fallax*. The largest decrease was for *S. canadensis* var. *hargeri* dropping from 76% to 67% correct placement a posteriori.

One hexaploid specimen from New Brunswick was unassigned to an a priori group so that it was not used in the Stepwise Discriminant Analysis and the generation of the discriminant functions used to assign specimens a posteriori. This specimen was included in the Classificatory Discriminant Analysis and placed in *Solidago lepida* var. *lepida* with 100% probability.

The results of the canonical analysis are shown in Figure 1. Eigenvalues for first three canonical axes were 3.022, 1.048, and 0.838.

Solidago brendiae and S. canadensis analysis

Data on the 74 *Solidago brendiae* and *S. canadensis* specimens were used to generate a pair-wise Pearson Correlation Matrix. The following pairs of traits had correlations greater than |0.7|: CAPL–CAPW, RPAPL–DCORL, RPAPL–DPAPL, and DCORL–DPAPL. DCORL and DPAPL were excluded in the discriminant analyses. CAPL and CAPW were also excluded as these were used to partially define a priori groups. Stepwise discriminant analysis selected the following four traits as useful in separating the a priori groups in the analysis including all taxa: RAYNUM (44.68), ULFLN (25.12), ULFSERNUM (9.98), and INVOLHT (8.63) in decreasing order of F-to-remove value. Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The between group F-matrix (df= 5 68) included just the one value of 44.678; Wilks' lambda = 0.2657, df = 4, 1, 72; approx. F= 44.6777, df = 4, 69; prob = 0.0000.

In the Classificatory Discriminant Analysis, the percent of correct assignments of specimens for *Solidago brendiae* and *S. canadensis* were 96% for each. Twenty-two of 23 specimens assigned a priori to the *S. brendiae* were placed a posteriori into *S. brendiae*; 17 specimen with 98-100% probability, three with 90-93% probability, and two with 81% and 89%% probability. One specimen of *S. brendiae* was assigned a posteriori to *S. canadensis* with 82% probability; this specimen was

from east of Escomins, Quebec, near the St. Lawrence River and had a damaged upper stem that distorted inflorescence development. Forty-nine of 51 specimens assigned a priori to the *S. canadensis* were placed a posteriori into *S. canadensis*; 39 specimen with 97-100% probability, six with 90-96% probability, and two with 74% and 81%% probability; and two with 52% and 56% probability. Two specimens were assigned a posteriori to *S. brendiae* with 95% (Georgian Bay, Ontario) and 77% (New York) probability.

A two dimensional plot of the number of ray florets verses the upper leaf length for specimens of *Solidago brendiae* and *S. canadensis* (including both varieties) is shown in Figure 2.

Solidago brendiae, S. canadensis var. canadensis, and S. canadensis var. hargeri analysis

Data on the 74 *Solidago brendiae* and the two varieties of *S. canadensis* specimens were used to generate a pair-wise Pearson Correlation Matrix. The following pairs of traits had correlations greater than |0.7|: CAPL–CAPW, RPAPL–DCORL, RPAPL–DPAPL, and DCORL–DPAPL. DCORL and DPAPL were excluded in the discriminant analyses. CAPL and CAPW were also excluded as these were used to partially define a priori groups. Stepwise discriminant analysis selected the following six traits as useful in separating the a priori groups in the analysis including all taxa: RAYNUM (27.52), MLFW (17.11), ULFL (8.26), INVOLHT (7.29), ULFSERNUM (5.66), and DLOBL (4.99) in decreasing order of F-to-remove value. Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all three groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 5.

Table 5. F-matrix for the discriminant analysis of *Solidago brendiae*, *S. canadensis* var. *canadensis*, and *S. canadensis* var. *hargeri*; df = 6 66.

	brendiae	***canadensis***	***hargeri***
brendiae	0.000		
canadensis	24.078	0.000	
hargeri	24.666	10.920	0.000

Wilks' lambda = 0.1394 df = 6 2 71; Approx. F= 18.4579 df = 12 132; prob = 0.0000

In the Classificatory Discriminant Analysis, the percent of correct assignments of specimens for *Solidago brendiae*, *S. canadensis* var. *canadensis*, and *S. canadensis* var. *hargeri* were 96%, 97%, and 86%, respectively. Twenty-three of 24 specimens assigned a priori to the *S. brendiae* were placed a posteriori into *S. brendiae*; 18 specimens with 96-100% probability, four specimens with 77-88% probability, one specimen with 67% probability, and one specimen with 38% probability (37% to var. *hargeri*, 25% to var. *canadensis*). One specimen of *S. brendiae* was assigned a posteriori to *S. canadensis* var. *hargeri* with 57% probability, to *S. brendiae* with 22% probability, and to *S. canadensis* var. *canadensis* with 21% probability; this was again the specimen was from east of Escomins, Québec. Twenty-eight of 29 specimens assigned a priori to *S. canadensis* var. *canadensis* were placed a posteriori into var. *canadensis*; 15 specimens with 90-100% probability, eight specimens with 71-84% probability, and one specimen with 69% probability (31% to var. *hargeri*). Again the Georgian Bay, Ontario, specimen was assigned to *S. brendiae* with 79% probability. Eighteen of 21 specimens assigned a priori to the *S. canadensis* var. *hargeri* were placed a posteriori into var. *hargeri*; 10 specimen with 90-100% probability, three specimens with 74-87% probability, and five specimens with 52-58% probability (48-42% to var. *canadensis*). One greenhouse grown voucher specimen of a New York collection was assigned a posteriori to *S. brendiae* with 71% (27% to var. *hargeri*). Two specimens assigned a priori to var. *hargeri* were assigned a posteriori to var.

canadensis with 81% and 71% probabilities. Two naturalized specimens of var. *hargeri* collected in the greater Zürich area, Switzerland, were placed a posteriori in var. *hargeri* with 89% and 52% probability.

Table 6. Results of the Classificatory Discriminant Analysis of the *S. brendiae/S. canadensis* complex.

Classification matrix (a priori assignments in rows, a posteriori assignments in columns).

	brendiae	***canadensis***	***hargeri***	**% correct**
brendiae	23	0	1	96
canadensis	1	28	0	97
hargeri	1	2	18	86
Totals	25	30	19	93

Jackknifed Classification matrix

	brendiae	***canadensis***	***hargeri***	**% correct**
brendiae	22	0	2	92
canadensis	2	28	0	97
hargeri	2	7	13	62
Total	24	35	15	85

The results of the canonical analysis are shown in Figure 3. Eigenvalues for first two canonical axes were 2.622 and 0.980.

Solidago brendiae and S. fallax analysis

Data on the 54 *Solidago brendiae* and *S. fallax* specimens were used to generate a pair-wise Pearson Correlation Matrix. The following pairs of traits had correlations greater than |0.7|: MLFLN–ULFLN, MLFW–ULFW, CAPL–CAPW and RPAPL–DPAPL. ULFLN, and RPAPL were excluded in the discriminant analyses. MLFW, ULFW, CAPL, and CAPW were excluded as these were used to define a priori groups. Stepwise discriminant analysis selected the following five traits as useful in separating the a priori groups in the analysis including all taxa: DPAPL (41.34), ULFSERNUM (29.12), INVOLHT (12.06), MLFLN (6.007), and RAYNUM (5.03) in decreasing order of F-to-remove value. Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all three groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The between group F-matrix (df= 13, 34) included just the one value of 21.441; Wilks' lambda = 0.3093, df = 5, 1, 52; approx. F= 21.4407, df = 5, 48; prob = 0.0000.

Table 7. F-matrix for the discriminant analysis of *Solidago brendiae*, *S. fallax* var. *fallax*, and *S. fallax* var. *molina*; df = 4 48.

	brendiae	*fallax*	*molina*
brendiae	0.000		
fallax	10.293	0.000	
molina	25.830	4.139	0.000

Wilks' lambda = 0.2590 df = 4, 2, 51; Approx. F= 11.5773 df = 8 96; prob = 0.0000

In the Classificatory Discriminant Analysis, the percent of correct assignments of specimens for *Solidago brendiae* and *S. fallax* were 96% and 90%, respectively. Twenty-three of 24 specimens

assigned a priori to *S. brendiae* were placed a posteriori into *S. brendiae*; 12 specimen with 100% probability, five with 96-99% probability, three with 83-87%, and three 70%, 62%, and 52% probability. One specimen of *S. brendiae* from Red Lake, Ontario was assigned a posteriori to *S. fallax* with 92% probability. Twenty-two of 24 specimens assigned a priori to the *S. fallax* were placed a posteriori into *S. fallax*; 15 specimens with 99-100% probability, seven with 92-97% probability, and two 78% and 66% probability. Three specimens assigned a priori to *S. fallax* were assigned a posteriori to *S. brendiae* with 91% probability (Saint-Gabriel, Québec and probably should have been assigned a priori to *S. brendiae*), 52% probability (Lark Harbour, west coast of Newfoundland with leaves intermediate in width between the two species), and 51% probability (Gros Morne Mt., Newfoundland).

Table 8. Results of the Classificatory Discriminant Analysis of *Solidago brendiae*, *S. fallax* var. *fallax*, and *S. fallax* var. *molina*.

Classification matrix (a priori assignments in rows, a posteriori assignments in columns)

	brendiae	***fallax***	***molina***	**% correct**
brendiae	20	4	0	83
fallax	1	9	2	75
molina	0	5	13	72
Total	21	18	15	78

Jackknifed classification matrix

	brendiae	***fallax***	***molina***	**% correct**
brendiae	19	5	0	79
fallax	1	9	2	75
molina	1	5	12	67
Total	21	19	14	74

A two dimensional plot of disc floret pappus length at anthesis versus the number of upper leaf serrations (one side of leaf) for specimens of *Solidago brendiae* and *S. fallax* (including both varieties) is shown in Figure 4.

Solidago brendiae, S. fallax var. fallax and S. fallax var. molina analysis

Fifty-four specimens of *Solidago brendiae*, *S. fallax* var. *fallax*, and *S. fallax* var. *molina* were included in the analysis. The following pairs of traits had correlations greater than |0.7|: MLFLN–ULFLN, MLFW–ULFW, CAPL–CAPW, and RPAPL–DPAPL. ULFL and RPAPL were not used in further analyses. MLFW, UPLW, CAPL, and CAPW were excluded from the analysis because the traits were used in defining a priori groups. Stepwise discriminant analysis selected the following traits as useful in separating the a priori groups in the analysis: DPAPL (20.09), ULFSERNUM (12.54), RAYNUM (7.87), and INVOLHT (5.90) in decreasing order of F-to-remove value. Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of the same group had probabilities of $p = 0.000$ that the null hypothesis was true.

In the Classificatory Discriminant Analysis, the percent of correct assignments of specimens a posteriori for *Solidago brendiae*, *S. fallax* var. *fallax*, and *S. fallax* var. *molina* were 83%, 75%, and 72%, respectively. Twenty of the 24 specimens of *S. brendiae* were assigned a posteriori to *S. brendiae* with 15 specimens assigned with 92-100%, and four assigned with 75%, 75%, 60% and

48%. Four specimens of *S. brendiae* were assigned a posteriori to *S. fallax* var. *fallax* with 66% (17% each to S. *brendiae* and var. *molina*; from the Chibougamau area, northwestern Québec), 62% (32% to var. *molina*; from Red Lake, Ontario), 60% (31% to *S. brendiae*, 9% to var. *molina*; from the Chibougamau Park, Québec), and 45% probability (38% to *S. brendiae* and 17% to *S. fallax* var. *molina*; this was the damaged specimen from Escomins, Québec). Ten of the 12 specimens of *S. fallax* var. *fallax* were assigned a posteriori to var. *fallax* with one specimen assigned with 90% probability, four specimens with 76-83% probability, two specimens with 62-69% probability, and one with 46% probability (30% to var. *molina*, 24% to *S. brendiae*). Three specimens assigned a priori to *S. fallax* var. *fallax* were assigned to other taxa; two were assigned to var. *molina* with 85% and 77% probability and one was assigned to *S. brendiae* with 85% (the specimen from Saint-Gabriel, Québec). Thirteen of the 18 specimens assigned a priori to *S. fallax* var. *molina* were assigned a posteriori to var. *molina* with five specimens assigned with 92-98% probability, five with 81-84% probability, two with 74 and 78% probability, and one with 53% probability (47% to var. *fallax*). Five specimens assigned a priori to *S. fallax* var. *molina* were assigned a posteriori to var. *fallax* with 79%, 68%, 55%, 53% and 46% with most of the remaining smaller probabilities to var. *molina*. The two specimens with the lower probabilities of assignment to var. *fallax* were also assigned 23-24% to *S. brendiae* (a sparsely hairy lower stem, hexaploid specimen from the Gaspé, Québec).

The results of the canonical analysis are shown in Fig. 5. Eigenvalues for first two canonical axes were 2.50 and 0.1.88.

A two dimensional plot of disc floret pappus length at anthesis versus the number of upper leaf margin serrations (one side of the leaf) for specimens of *Solidago brendiae*, *S. fallax* var. *fallax*, and *S. fallax* var. *molina* is shown in Fig. 6.

Solidago canadensis var. canadensis and S. canadensis var. hargeri analysis

Fifty-one specimens of *Solidago canadensis* were included in the analysis; 30 var. *canadensis* and 21 var. *hargeri*. The following pairs of traits had Pearson correlations greater than |0.7|: CAPL–CAPW, RSTRAPL–DCORL, RPAPL–DCORL, RPAPL–DPAPL, and DCORL–DPAPL. RPAPL and DCORL were not used in further analyses. Stepwise discriminant analysis selected the following traits as useful in separating the a priori groups in the analysis including all taxa: ULFW (12.34), RAYNUM (8.17), DLOBL (7.00), MLFLN (6.81), ULFLN (5.03) and INVOLHT (4.61) in decreasing order of F-to-remove value. Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all three groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The between group F-matrix (df= 13, 34) included just the one value of 11.112; Wilks' lambda = 0.3976, df = 6, 1, 49; approx. F= 11.1123, df = 5, 44; prob = 0.0000.

In the Classificatory Discriminant Analysis, the percent of correct assignments of specimens a posteriori for *Solidago canadensis* var. *canadensis* and *S. canadensis* var. *hargeri* were 97% and 81%, respectively. Twenty-nine of the 30 (97%) of the var. *canadensis* specimens were assigned a posteriori to var. *canadensis* with 22 specimens with 90-100% probability, four specimens with 78-84% probability, and two specimens with 56% and 53% probability. One specimen was assigned a posteriori to var. *hargeri* with 83% probability. Seventeen of the 21 specimens of var. *hargeri* were assigned a posteriori to var. hargeri with twelve specimens with 90-100% probability, three specimens with 78-82% probability, and one specimen with 54% probability (Fulton Co., Pennsylvania, voucher cultivated at WAT). Four specimens assigned a priori to var. *hargeri* were assigned a posteriori to var. *canadensis* with 90%, 77%, 56%, and 53% probabilities.

The results of the canonical analysis are shown as a histogram in Fig. 7. Eigenvalue for first two canonical axis was 1.515.

A two dimensional plot of upper leaf width versus the number of upper ray florets for specimens of *Solidago canadensis* var. *canadensis* and *S. canadensis* var. *hargeri* is shown in Fig. 8.

DISCUSSION

Seven taxa analysis

Based on the percents of correct assignments and the frequencies of high probabilities of those assignments, *Solidago brendiae*, *S. canadensis* var. *canadensis*, and *S. elongata* were fairly well supported as species with 0-4% decrease in correct a posteriori classification values between the linear and jackknifed analyses. *Solidago canadensis* var. *hargeri* had less support with a 9% decrease in correct a posteriori classification values for the two methods of classification. *Solidago lepida*, *S. fallax* var. *fallax*, and *S. fallax* var. *molina* had less support with correct a posteriori values of 63-67%. Most of specimens of *S. lepida* with a known chromosome number were hexaploid; those known to be diploids were placed with varying probabilities into mostly diploid *S. elongata*, and the mostly diploid *S. fallax*.

The traits with the higher F-to-remove values were not always characters known to be influenced by ploidy level (Heard & Semple 1988; Semple et al. 1990; Semple & Cook 2006). Involucre height, which is strongly influenced by ploidy level in *Solidago* was only a lower level differentiating character. Involucre height was critical in separating *S. lepida* from diploid or possibly diploid specimens of *S. fallax* var. *molina* in northern Ontario. Involucre height also may explain why diploid specimens of *S. lepida* from western Canada and the USA were atypical for this sample of the species and were misplaced into *S. elongata*. At the species level, 20 of 27 specimens of *S. fallax* (74%) were assigned a posteriori to the species indicating support for recognizing the species, but specimens of the two varieties of *S. fallax* were assigned to each other with sometimes low probabilities indicating less support for recognizing the varieties. Additional analyses of the western taxa are needed to resolve the western problems and are not included here.

Noted in the Results was the inclusion of two specimens of *S. elongata* from British Columbia. Semple and Cook (2006) did not list the species as being present in Canada.

A hexaploid specimen from the Gaspé, Quebec, assigned a priori to *Solidago fallax* var. *molina* was assigned a posteriori to *S. lepida*. Lower stem pubescence of this plant was very sparsely villous-strigose as were some of the *S. lepida* plants from northern Ontario. Such plants may just be more hairy than normal *S. lepida*. Some of the hexaploid western specimens of *S. lepida* were assigned to *S. fallax* var. *molina* but with low probability. No hairy-stemmed race of *S. lepida* has been described to date. Additional research is needed on a larger sample size or with molecular techniques to determine whether or not describing a new hairy-stemmed taxon in *S. lepida* would be justified, as appears to be the case for *S. canadensis* var. *hargeri* and *S. fallax* var. *molina*.

Support for the new species *Solidago brendiae* was higher than expected considering how many taxa have been described in the *S. canadensis*/*S.lepida* complex and that no one recognized *S. brendiae* as a distinct taxon previously. This might also be the result of a long period of lumping by botanists such as Arthur Cronquist following Fernald's splitting of taxa in 1915. Someone who felt that it was reasonable to treat *S. lepida* as a variety of *S. canadensis* would not be likely to look for ways to split up the eastern portion of the *S. canadensis*/*S. lepida* complex into more species. The involucres of *S. brendiae* are taller than those of *S. canadensis*; both taxa are only known at the diploid level so the difference is not a of ploidy level effect.

In the field in 2006, some collections of *Solidago brendiae* made by JCS were obviously not *S. fallax* and obviously not *S. canadensis* based on leaf width, nature of the leaf serrations and leaf surface features (shiny or not). Preliminary analyses with a smaller data set of specimens mostly

from the northern Gaspé had higher percents of correct placement values for *S. brendiae*, but also included specimens with lower percent probabilities of placement for specimens treated as *S. fallax* and *S. canadensis* or when treated as *S. brendiae* in other analyses. When the sample size of *S. brendiae* was more than doubled with additional specimens being scored and when some of those possible *S. brendiae* specimens from elsewhere in Quebec, Newfoundland, New Brunswick, Nova Scotia and Prince Edward Island were re-assigned to *S. brendiae*, then the variances of canonical scores decreased significantly for *S. brendiae* even as the ranges of character variation increased for some traits. Specimens from Nova Scotia and Prince Edward Island that had been assigned with low probabilities or ambivalently to *S. brendiae*, *S. canadensis*, or *S. fallax*, became specimens assigned to *S. brendiae* with much higher probabilities following the expansion of the sample to include the full range of variation of traits occurring in the species. As the understanding of Fernald's eastern "*elongata*" emerged, correct placements improved as the matrix was repeatedly expanded over several years.

In the diagram plotting canonical scores (Fig. 1), *Solidago brendiae* specimens are not strongly separated from other taxa in the middle of the diagram potting the first and second canonical scores, but on the plot of the first versus the third canonical scores many of the *S. brendiae* specimens are separated out from the central core of *S. fallax* and *S. lepida* specimens. This illustrates the generally larger F-matrix values separating *S. brendiae* from most other taxa in the seven taxon analysis (Table 2). The analyses are done based on distances between specimens plotted in seven dimensions, which obviously cannot be visualized. The canonical reduction method is thus only a reflection of what the statistics are really showing. In the case of *S. brendiae*, the statistics indicate that the taxon is sufficiently distinct to warrant species level recognition.

The decision to treat *Solidago brendiae* and *S. fallax* as species was also reached following a shift in species concept as applied to *Solidago* (Semple 2012; Semple et al. 2012; Semple & Peirson 2013; Peirson et al. 2013). In this case, the result is a breaking up of what had been a multi-taxon *S. lepida* (Semple & Cook 2006) into eastern and western groups of species (Semple 2013). While Cronquist (1994) continued to lump taxa into larger multi-race species, Semple (Astereae Lab web site) has moved to deCronquistify *Solidago* by recognizing many more narrowly defined species with different ecological preferences. The latter approach is in line with recent molecular data (Peirson et al. 2013) followed by Semple and Peirson (2013) in subsect. *Humiles*.

Additional analyses were performed to compare *Solidago brendiae* with diploid eastern species with which it can be confused. Removing *S. lepida* and *S. elongata* from the comparisons ensured that additional useful characters besides those used to define *S. brendiae*, *S. canadensis*, and *S. fallax* could be found via stepwise discriminant analyses. These additional analyses are discussed below.

Solidago brendiae and S. canadensis analysis

In this analysis, four characters were found to be useful in separating *Solidago brendiae* and *S. canadensis* (96% correct placement a posteriori for both species). Assignment to a priori group was based on differences in the appearance of the array of heads in the two species illustrated in Ill. 1. The *S. brendiae* shoot in Fig. 9A has a much leafier inflorescence array with more ascending branches; this is more similar to *S. fallax* than to *S. canadensis*. The most important characters in terms of size of the F-to-remove values were upper leaf length and the number of ray florets per head (see Fig. 2). Specimens of *S. brendiae* that had shorter upper leaves had the most ray florets (more than 14) well outside the range of *S. canadensis*, while specimens of *S. brendiae* with fewer ray florets had the longest upper leaves well outside the range of *S. canadensis*. These traits in combination with the appearance of the inflorescence array separates the two species in nearly all cases.

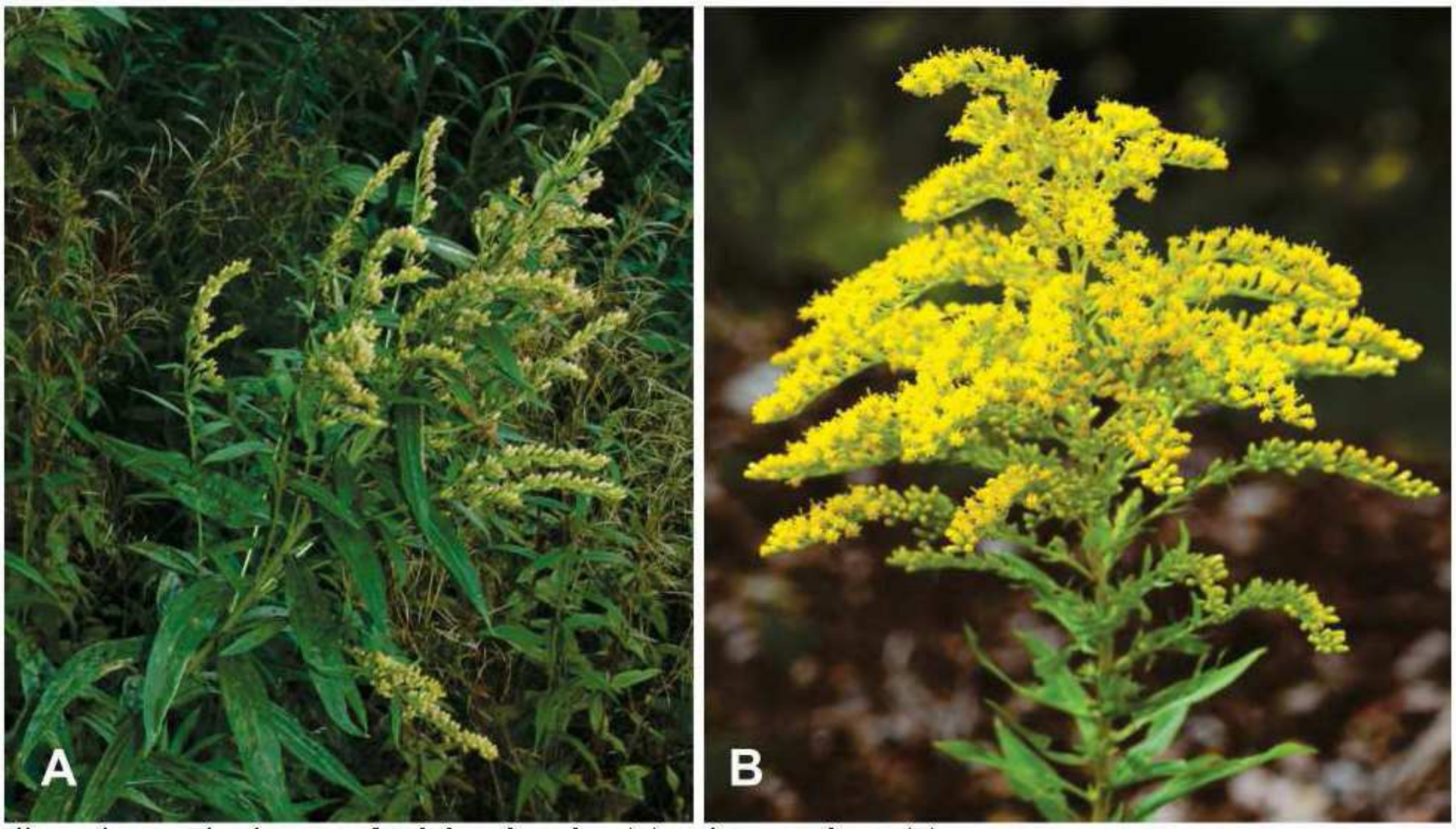

Illustration 1. Floral arrays of *Solidago brendiae* (A) and *S. canadensis* (B).

Solidago brendiae, S. canadensis var. canadensis, and S. canadensis var. hargeri analysis

The results of this analysis indicate that *Solidago brendiae* is about equally different from the two varieties of *S. canadensis*, but the two varieties are much less so different from each other based on the F-matrix values (Table 5).

Solidago brendiae and S. fallax analysis

The results of this analysis indicate that *Solidago brendiae* is distinct from *S. fallax* but not as well-supported as in the comparison of *S. brendiae* and *S. canadensis* based on the F-matrix values in the two analyses and the percents of correct a posteriori placement. This suggests that *S. brendiae* last shared a common ancestor with *S. fallax*, but confirmation of this hypothesis will require molecular approaches and a true phylogenetic methodology. Multivariate methods are useful in defining group limits but are not designed to resolve phylogenetic relationships.

Solidago brendiae, S. fallax var. fallax and S. fallax var. molina analysis

Disc floret pappus length at anthesis was determined to the best character separating *Solidago brendiae* and the two varieties of *S. fallax* followed by the number of upper leaf margin serrations. Mid and upper stem leaf width was used to define *S. brendiae* a priori in this analysis so it was not used in the discriminant analysis, leaving less obvious and clearly more technical characters to distinguish the taxa. Of note is the result that specimens var. *molina* was much more likely to be assigned a posteriori to var. *fallax* than were specimens of var. *fallax* assigned to var. *molina*. Values of percents of correct a posteriori assignment to variety in *S. fallax* were much lower (75% and 72%) than in the case of the varieties of *S. canadensis* (97% and 86%), although in both analyses assignment to varieties was based on just the density of hairs on the lower portion of the stem.

Solidago canadensis var. canadensis and S. canadensis var. hargeri analysis

Support for recognizing two varieties in *Solidago canadensis* was strong. Six traits were selected as useful in separating var. *canadensis* and var. *hargeri*, but with only one trait mid leaf

length (MLFLN) having a F-to-remove value greater than 10. Assignment to each variety was based on the absence or presence of lower stem pubescent. The height at which the stem became obviously moderately to densely pubescent varied considerably. This is ambiguity in defining the two varieties is compounded by the observation that in subsect. *Triplinerviae*, larger thick older lower stems sometimes lose their pubescence with age, although a few hairs or scars still can indicated the more juvenile condition. The difference in the length of growing season between North Carolina and Wisconsin, southern Ontario and Québec might explain some of the difference between the mid and upper leaf size traits in the somewhat more northern var. *canadensis* and the somewhat more southern var. *hargeri*, but the ranges overlap considerably. Possibly resources used by the plant to make hairs influence floral traits by not being available for their development. A molecular approach to differentiating the two varieties is needed to resolve phylogenetic questions. This study clearly shows that there are morphological differences between the two varieties beyond just stem hairiness. The differences yield multivariate analysis results that are comparable to species level taxa included in this study. The first author is not comfortable with the idea that var. *canadensis* and var. *hargeri* should be treated as separate species. The degree of stem hairiness at different heights on the stem is variable in multiple species in subsect. *Triplinerviae* and in the genus overall. Without additional non-morphological data to support species level status of hairy and glabrous lower stem morphs, varietal recognition is seems sufficient.

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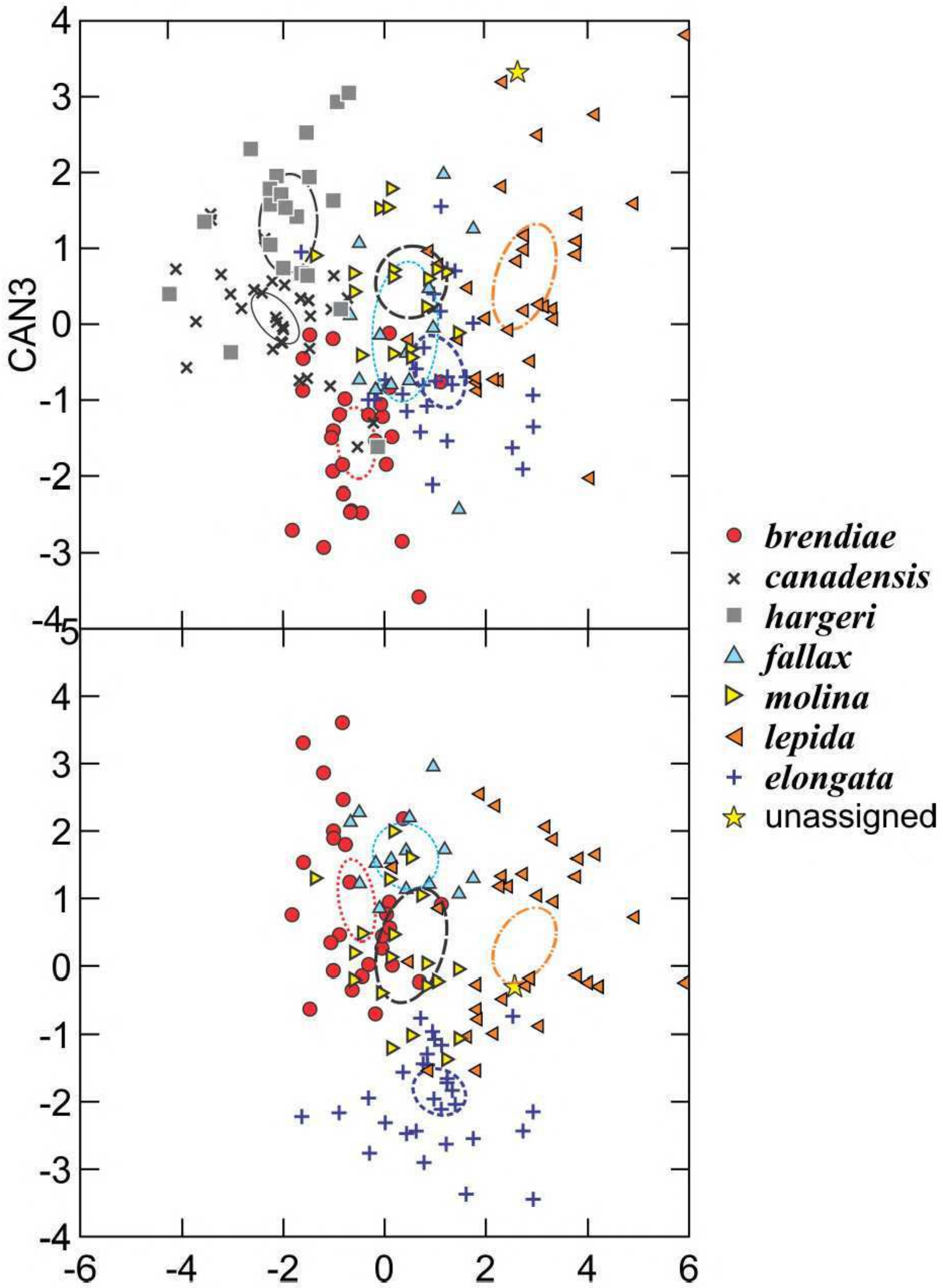

Figure 1. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores generated by the Canonical Analysis of specimens of the *Solidago canadensis/S. lepida* complex; 95% confidence ellipses are shown for each taxon.

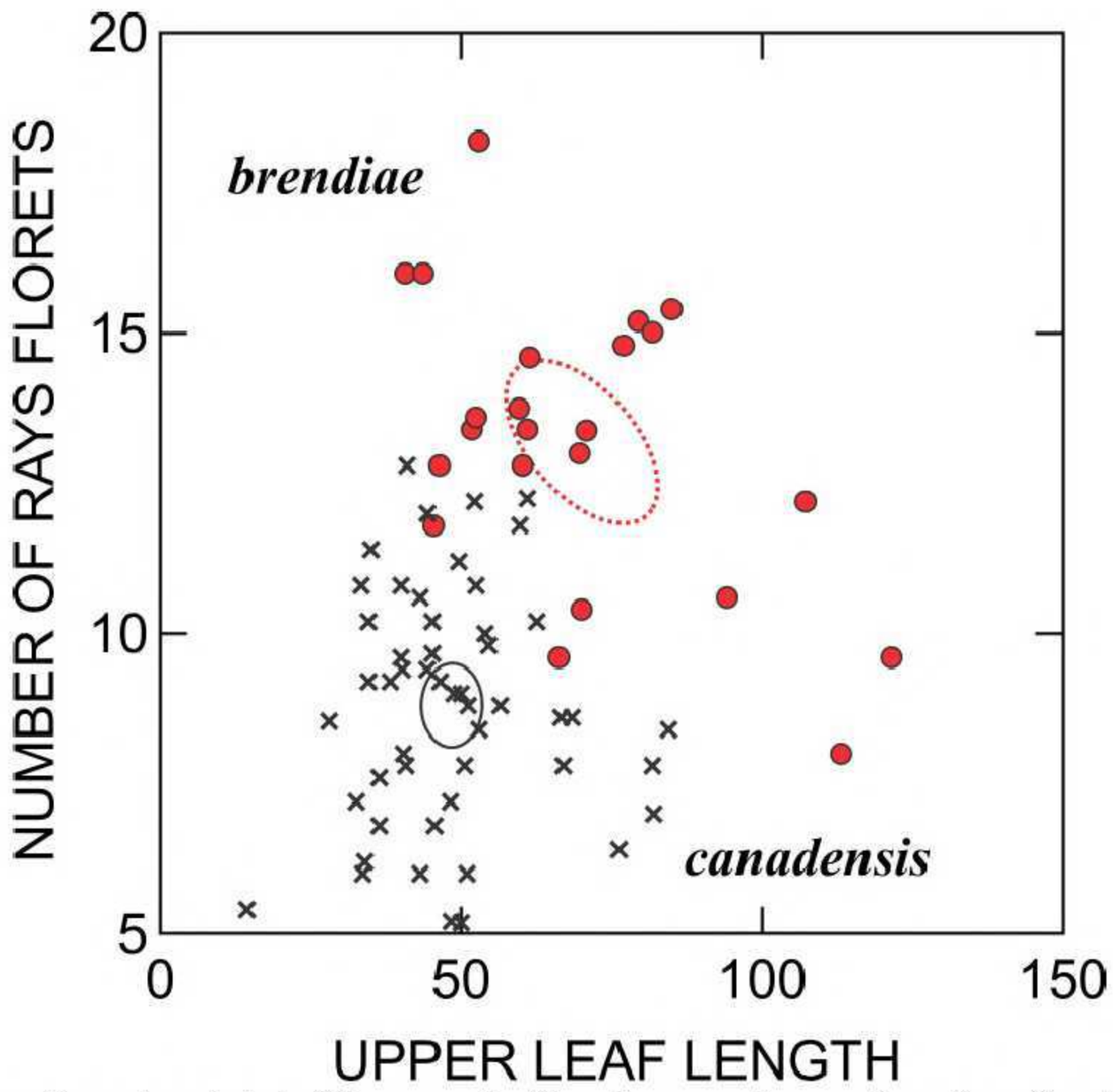

Figure 2. Two dimensional plot of the upper leaf length verses the number of ray florets for specimens of *S. brendiae* and *S. canadensis* (including both varieties); 95% confidence ellipses are shown for each taxon.

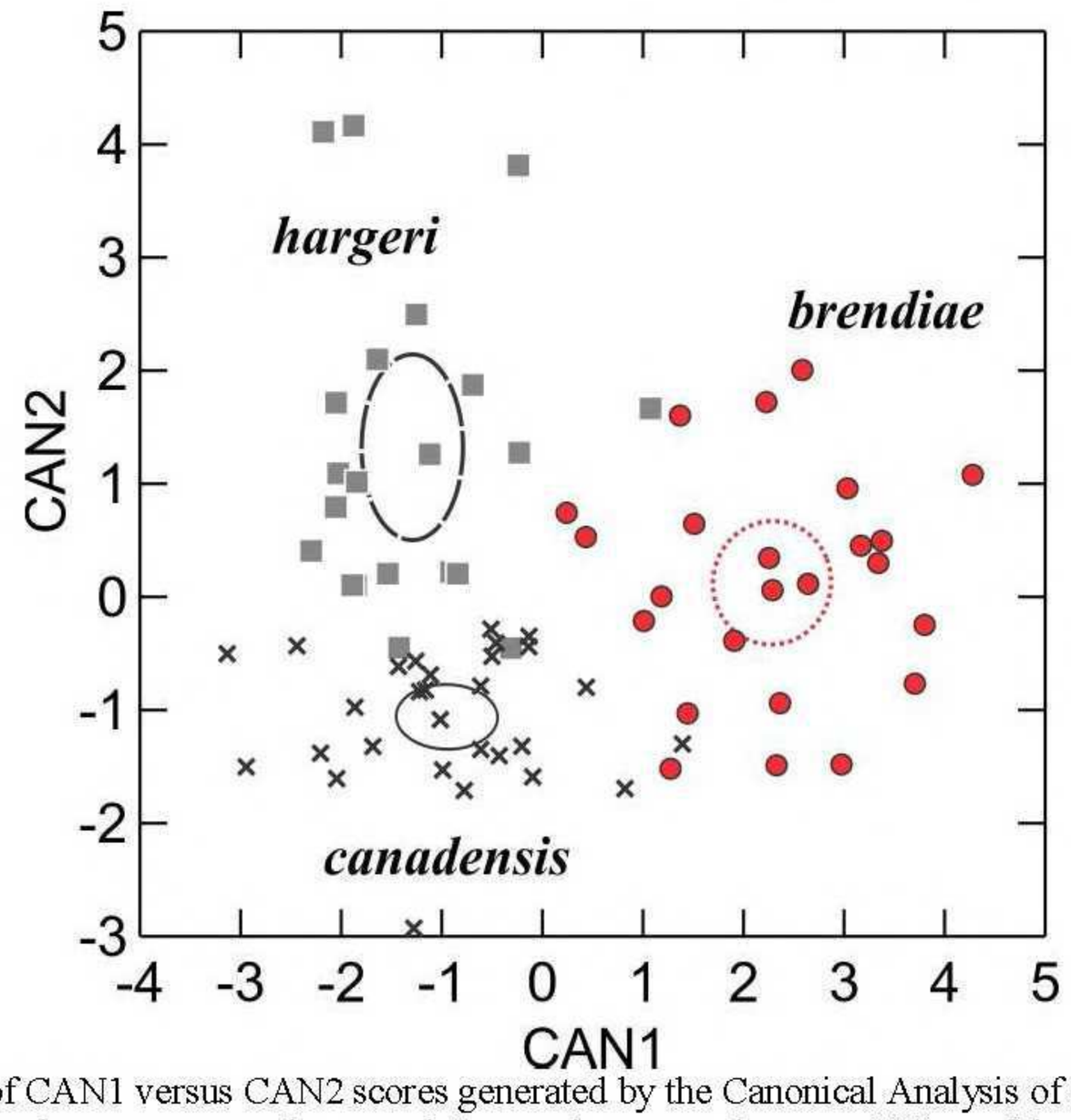

Figure 3. Plot of CAN1 versus CAN2 scores generated by the Canonical Analysis of specimens of *Solidago brendiae*, *S. canadensis* var. *canadensis* and *S. canadensis* var. *hargeri*; 95% confidence ellipses are shown for each taxon.

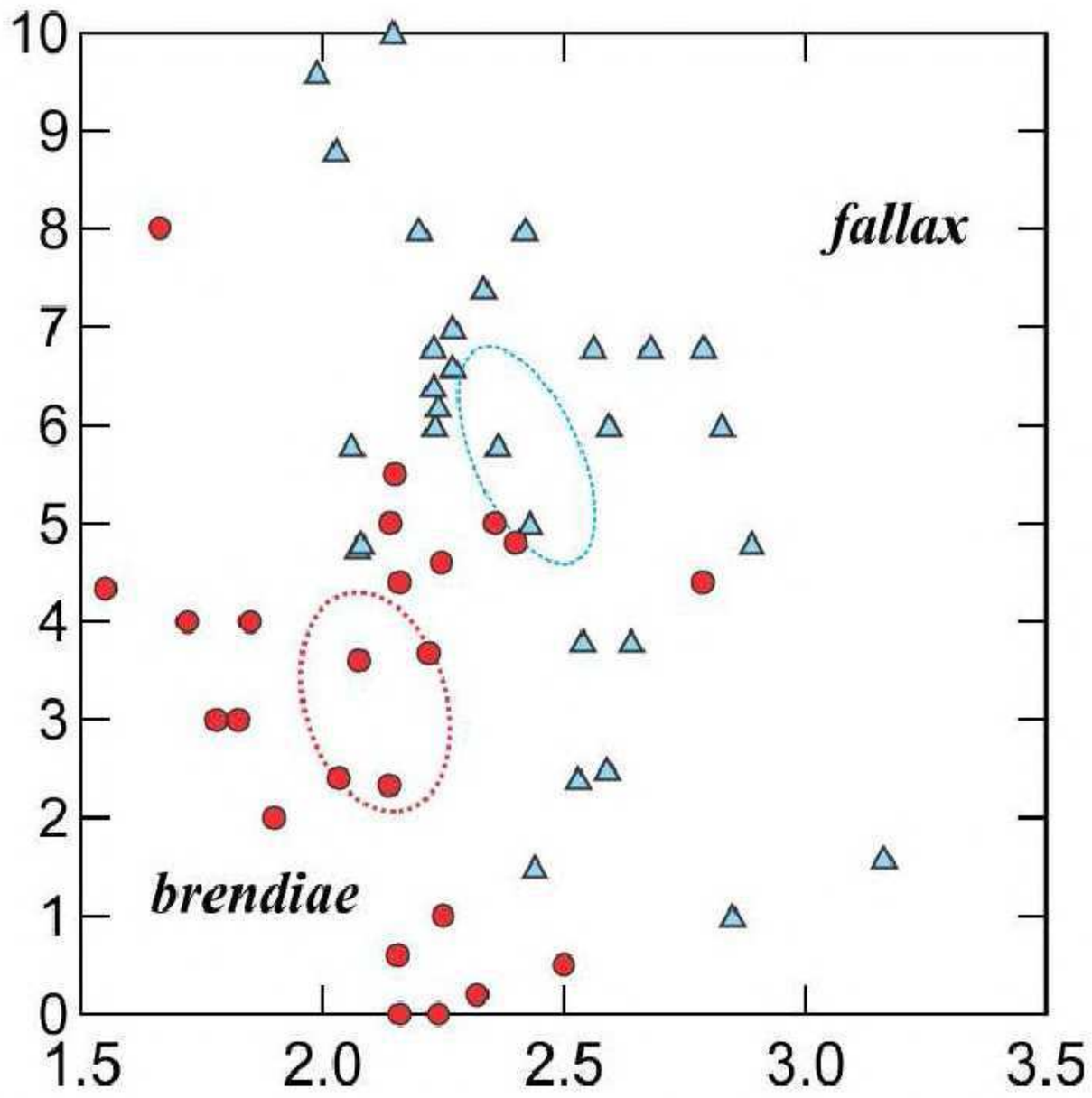

Figure 4. Plot of the number of upper leaf serrations (one side) versus number of ray florets for specimens of *S. brendiae* and *S. fallax*; 95% confidence ellipses are shown for each taxon.

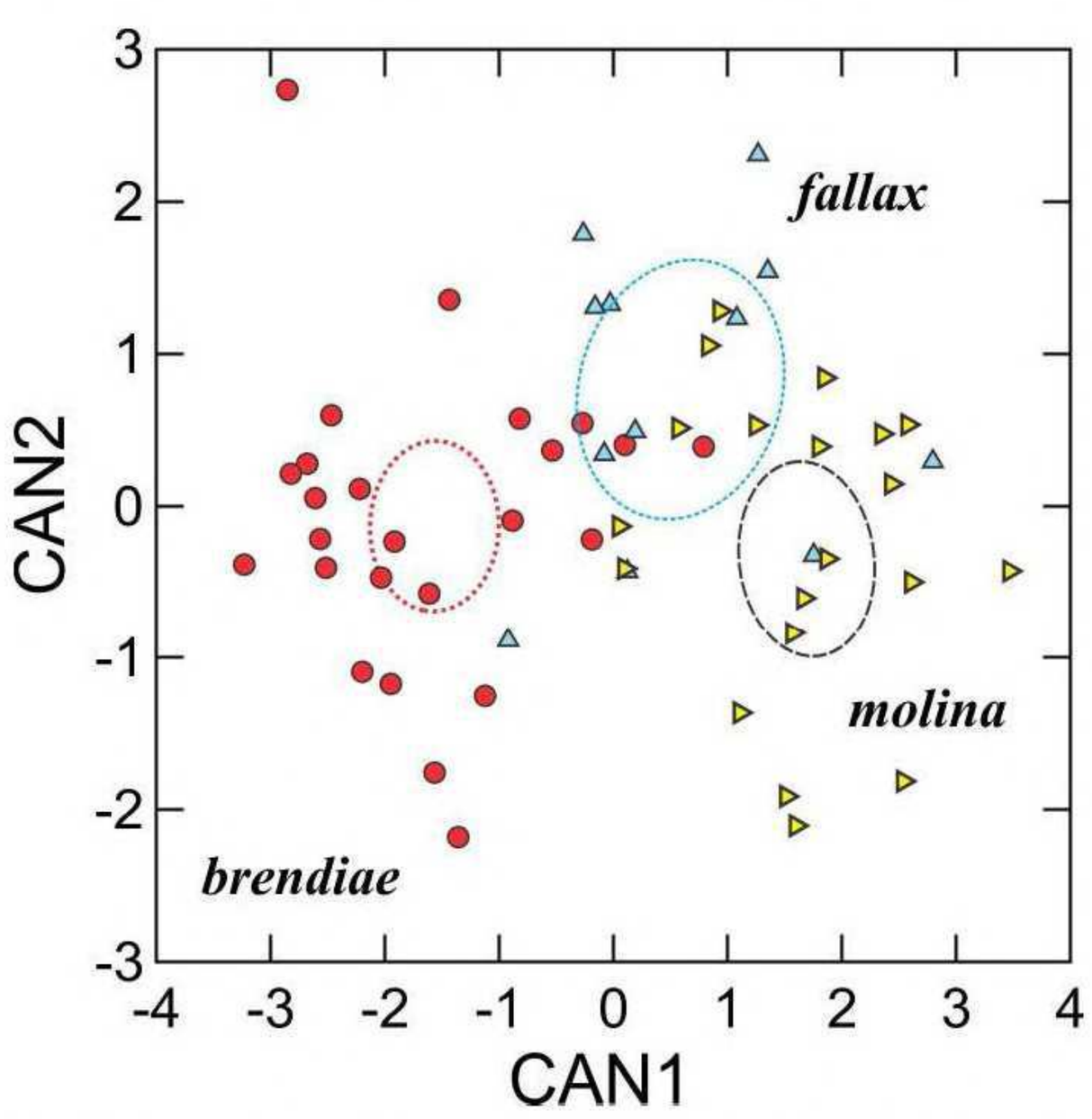

Figure 5. Plot of CAN1 versus CAN2 scores generated by the Canonical Analysis of specimens of *Solidago brendiae*, *S. fallax* var. *fallax* and *S. fallax* var. *molina*; the discriminant analysis did not include mid and upper leaf width traits used in defining a priori groups; 95% confidence ellipses are shown for each taxon.

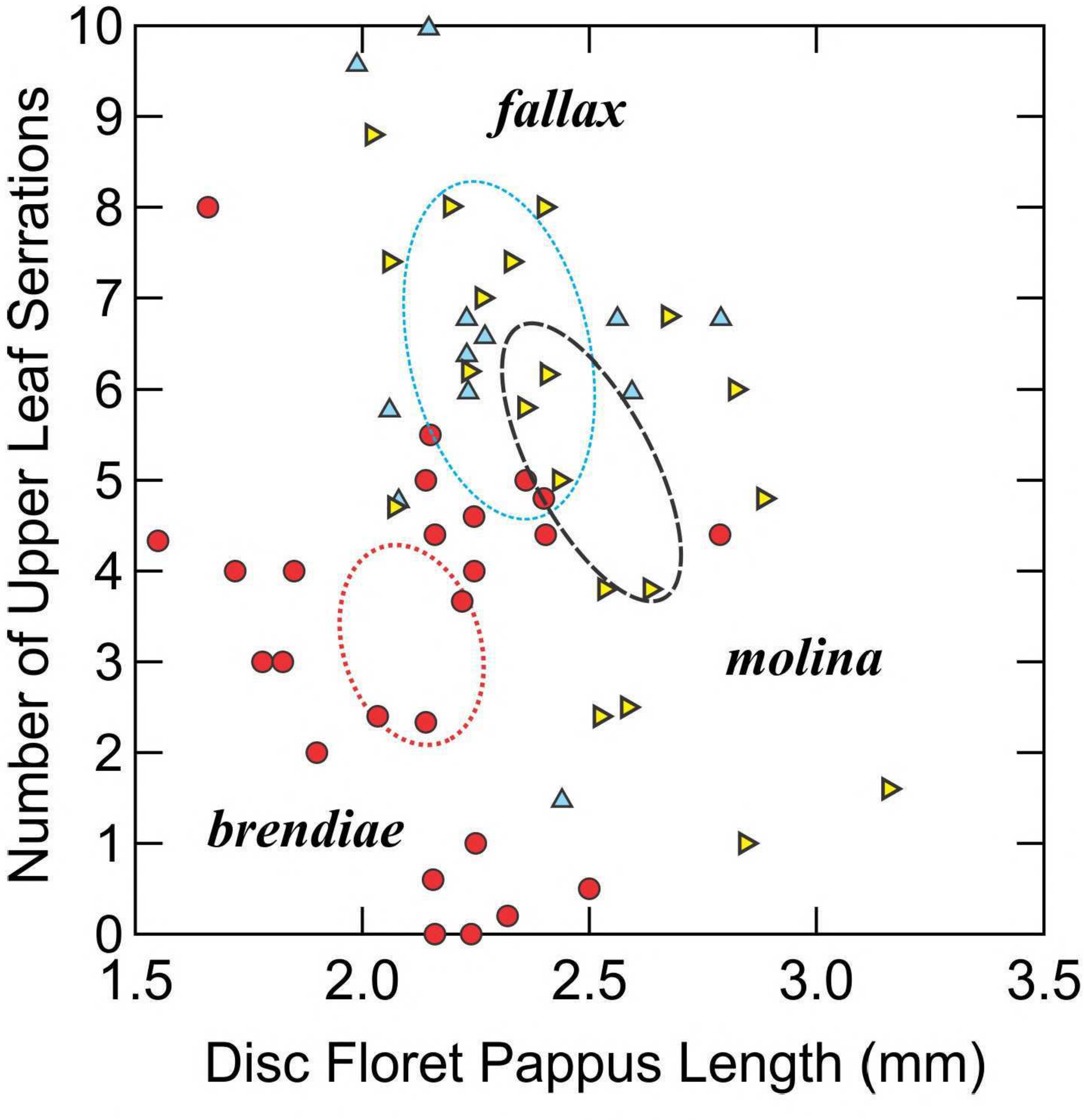

Figure 6. Two dimensional plot of the disc pappus length (anthesis) versus the number of upper leaf margin serrations (one side) for specimens of *Solidago brendiae*, *S. fallax* var. *fallax* and *S. fallax* var. *molina*; 95% confidence ellipses are shown for each taxon.

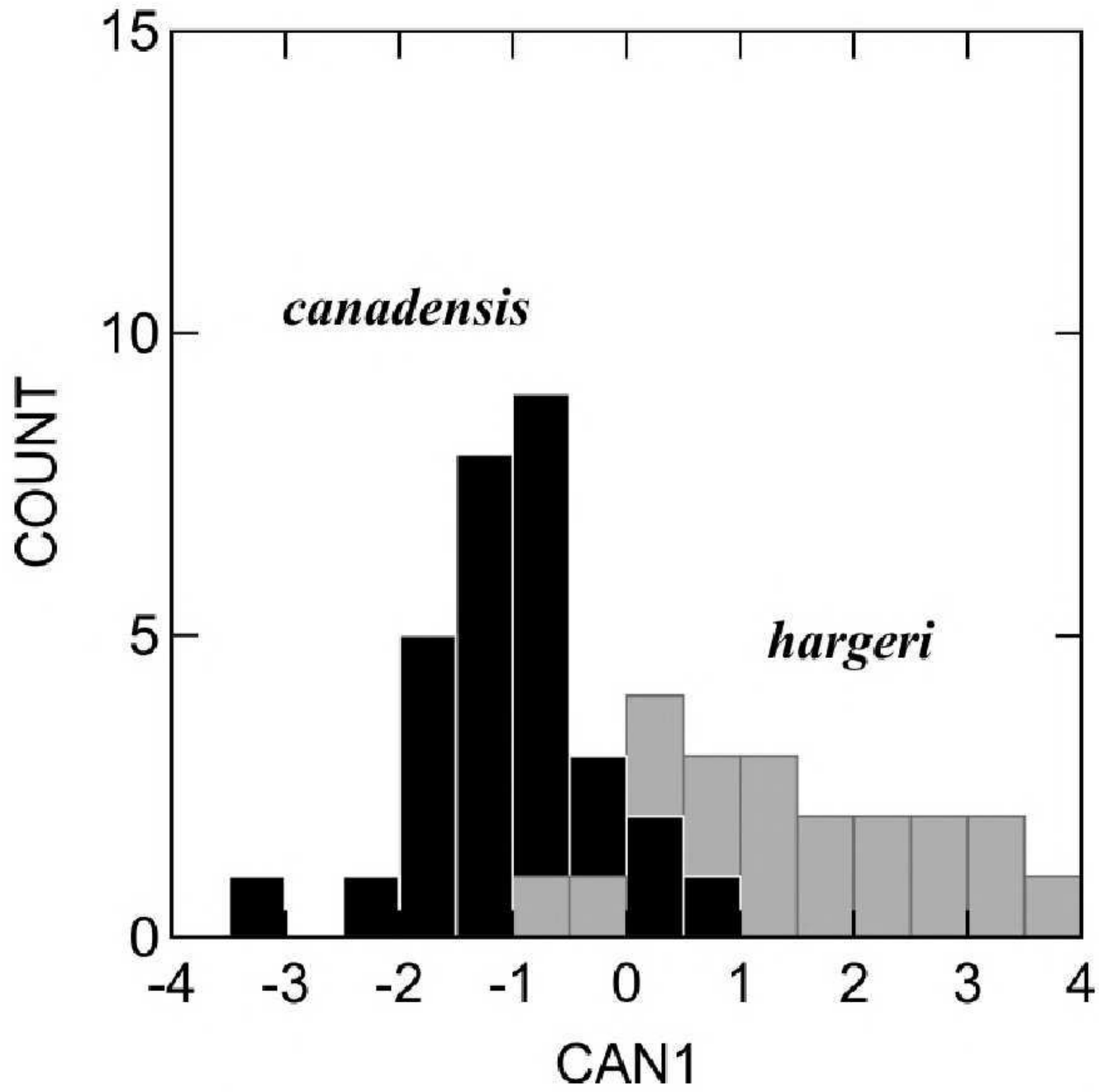

Figure 7. Histogram of CAN1 frequencies generated by the Canonical Analysis of specimens of *Solidago canadensis* var. *canadensis* and *S. canadensis* var. *hargeri*.

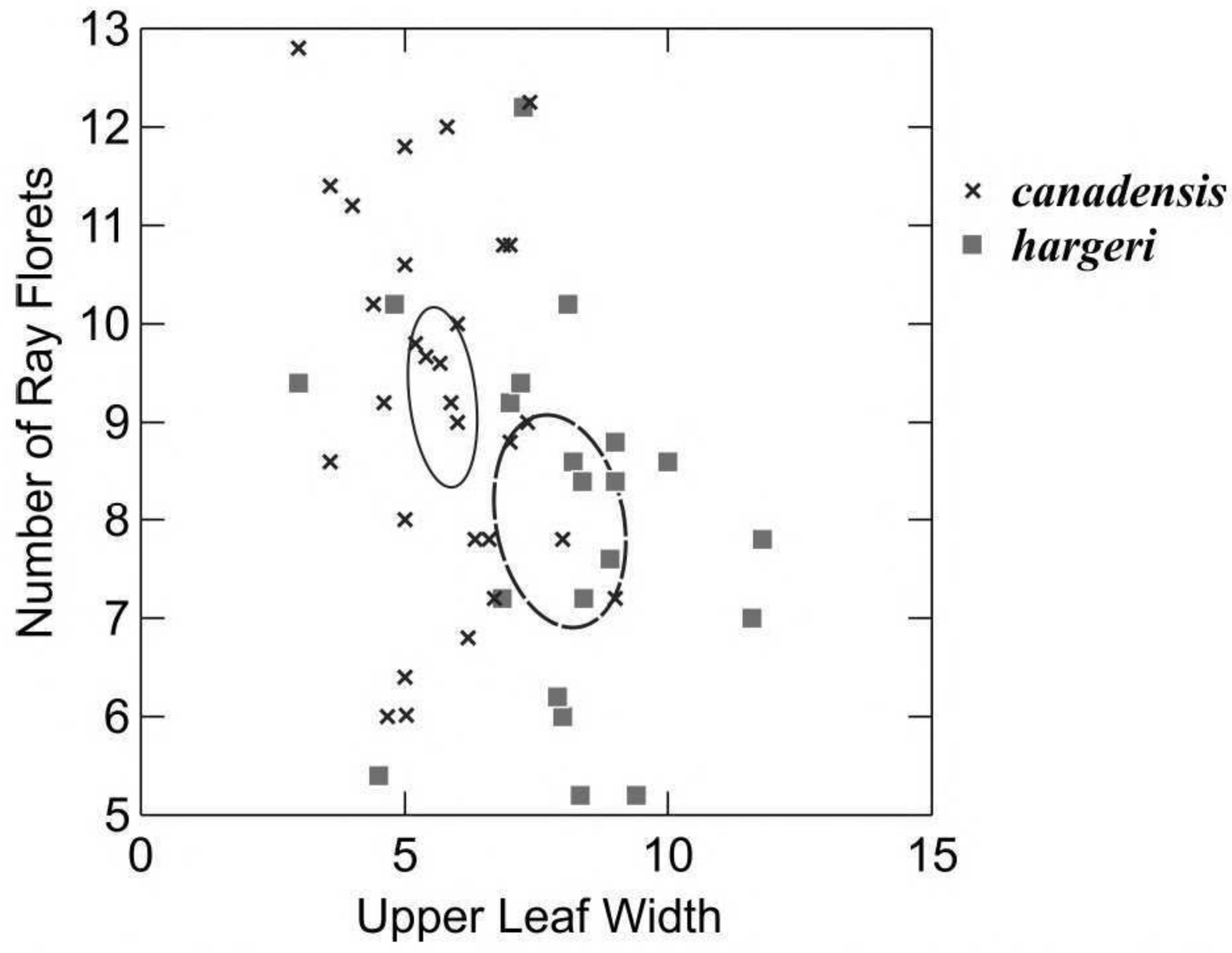

Figure 8. Plot of upper leaf width versus number of ray florets for specimens of *Solidago canadensis* var. *canadensis* and *S. canadensis* var. *hargeri*; 95% confidence ellipses are shown for each taxon.